

BREATHING MOVEMENTS OF THE CUBAN BURROWING COCKROACH¹

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Efforts to ascertain the effect of higher nerve centers upon insect respiration originated with Plateau (1884), who found that removal of brain tissue slowed respiratory movement in some insects. Bethe's (1897) belief has been substantiated in that the brain maintains muscle tonus through a directly facilitating homolateral connection with lower motor centers; the brain also regulates locomotor activity by inhibiting the subesophageal ganglion, which is a center that facilitates movement reflexes in the thorax. Bethe found that after removal of the brain in *Hydrophilus* and *Apis*, reflex responses become exaggerated and movements such as antenna cleaning may continue for hours.

Matula (1911) stated that in *Aeschna* naiads, activity of the ventral ganglia is under the influence of a cerebral breathing center. Alverdes (1926), however, found that each of the first five abdominal ganglia in *Cloeon* naiads contain a center which regulates respiration of the corresponding gills, and that maximum gill movement is possible only if the abdominal centers are connected to a center located in the sixth abdominal ganglion.

Further efforts to localize the centers controlling the breathing mechanism were made by Fraenkel (1932), in which the wasp, *Vespa*, was found to have its respiratory center in the thorax; no coordinated breathing movements were demonstrated in the isolated abdomen. Schreuder and de Wilde (1952) concluded that pre-anesthetic respiratory movements originate from and are under the control of a thoracic ganglion in *Periplaneta americana*. Miller (1960) states that the metathoracic ganglion of the locust, *Schistocerca gregaria*, may contain a pacemaker which controls the frequency and amplitude of ventilation. The cockroach, *Blattella craniifer*, has its neural ventilative control center in the metathoracic and first abdominal ganglion, according to Case (1961).

This investigation utilizes the insect spiograph to record breathing movements of the Cuban burrowing cockroach, *Byrsotria fumigata*. The normal respiratory movements of the intact animal are compared with the exaggerated spontaneous respiratory movements which occur after extirpation of certain portions of this insect's nervous system. From this information the influence of higher nerve centers on the respiratory center is postulated, and a general location of the center is made.

METHODS

Adult females of *Byrsotria* used in this study weigh up to 7 g and are approximately 4.5 cm in length. These insects are easily cultured, lack the disagreeable odor characteristic of most cockroaches, and are quite tractable. The males are winged and are smaller than the nearly apterous females.

The insect spiograph is used to record the respiratory contractions of the abdomen which ventilate the tracheal system of the insect. Tracings of these movements are made on the smoked drum of a kymograph. The cockroach is held in an immobilization cage made of wire screening which approximates the dimensions of the insect and is open at the top and one end. Insect pins inserted through the screen across the body of the cockroach restrain gross body movements while allowing respiratory action to continue (Myers, 1958).

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A nylon thread sewn through the posterior edge of the fifth abdominal tergal sclerite of the insect is attached to the writing arm of a counter-balanced heart-lever which is adjusted to give approximately 18 mm depression of the lever-arm for each 1 mm lowering of the insect abdomen. The immobilization cage is placed inside a plastic ventilation chamber containing an air intake and outflow opening as well as a slit through which the cockroach may be connected to the lever-arm. Compressed air or CO₂ can be fed through separate flowmeters into a mixing tube from which the resulting gas is forced through the ventilation chamber. Filtering or moisturizing of the gas was found to be unnecessary. Over 300 hr of cockroach pneumography has been recorded by this method.

RESULTS

Response of Intact Roach

Spirograms taken from intact cockroaches during their quiescent periods show that breathing movements are not continuous, but rather that they occur in groups averaging 5 movements per group. Each of these "normal" respiratory movements last about 6 sec with the average group lasting about 30 sec. Were the insects to breathe continuously the movements would average 10 per min. The respiratory groups are, however, interspersed between periods of apnea averaging 7 min in duration (fig. 1). A typical quiescent female Cuban burrowing cockroach spends approximately 4 min of each hour ventilating its tracheal system while the remaining 56 min are apneous.

Response of the Decerebrated Roach

After brain excision, the respiratory pattern of the quiet cockroach slows to a frequency of 7 per min with respiratory groups of 5 to 30 movements per group. Periods of apnea averaging 3 min in duration occur between these groups. The amplitude of these intermittent groups may range up to 8 times greater than that of the intact roach. This periodic breathing (fig. 2) may continue for several days after brain removal.

Response of the Decapitated Roach

Upon removal of both supra- and subesophageal ganglia by decapitation, the frequency of respiratory movements remains at approximately 7 per min. These movements, however, are continuous except for an occasional brief period of apnea. The amplitude of this continuous breathing (fig. 3) may be as much as ten times that of the intact cockroach. These movements decrease in amplitude after about 30 hr but the rate is maintained for several days. Female Cuban burrowing roaches may live for over a month in the decapitated condition when maintained in an atmosphere of high humidity.

Response of the Isolated Abdomen

When the abdominal portion of the body of *Byrsotria* is separated from the thorax and is sealed off at a level between the metathoracic and first abdominal ganglion, respiratory movements continue in a pattern similar to that of the decapitated cockroach averaging 6 per min (fig. 4, upper line). The amplitude of these nearly continuous movements is small due to the limitation of movement imposed by the sealed anterior portion of the abdomen.

When an atmosphere containing CO₂ is forced over the isolated abdomen, spiograms show regular step-wise increases in ventilatory rate and in amplitude. Rate increases from the continuous 6 per min frequency of the unstimulated abdomen to a 38 per min rate at 27 percent CO₂ (fig. 4, lower line).

DISCUSSION

The intact female *Byrsotria fumigata* breathes infrequently in its resting state (fig. 1) and probably relies heavily upon diffusion for the exchange of gases in its

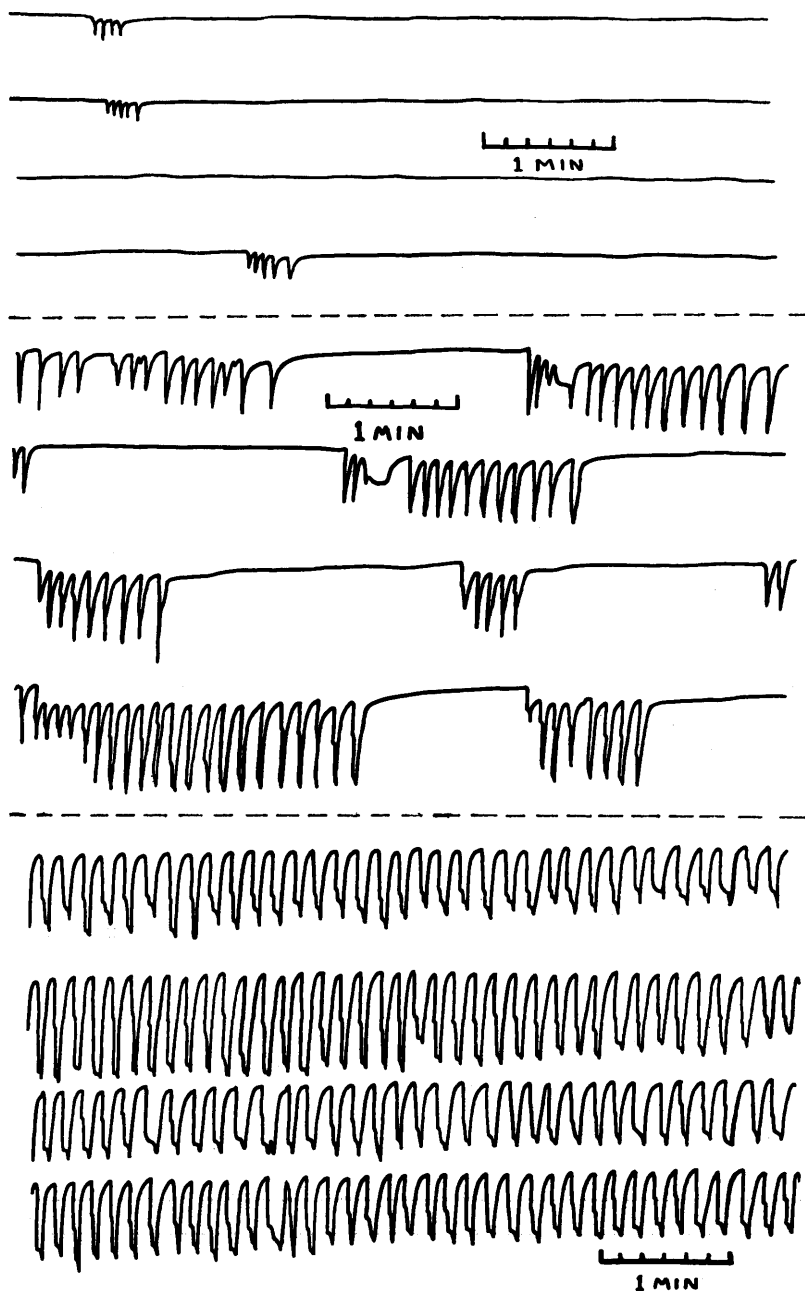


FIGURE 1 (top). Spirogram of quiescent female Cuban burrowing cockroach showing widely separated bursts of ventilatory movements averaging 10 movements per min.

FIGURE 2 (middle). Characteristic spiogram of quiescent decerebrated cockroach showing alternation of slow spontaneous respiratory movements with periods of apnea.

FIGURE 3 (bottom). Characteristic spiogram of quiescent decapitated cockroach. These slow uninterrupted spontaneous movements may continue for several days.

tracheal system. This cockroach is, however, not apneous when quiescent as is the American cockroach (Schreuder and de Wilde, 1952).

The decerebrated cockroach has a respiratory pattern (fig. 2) consisting of a slow series of exaggerated movements occurring in groups separated by short periods of apnea. These spontaneous movements are believed to be the result of lowered inhibition of respiratory reflex centers in the abdominal ganglia. The brain, acting on the subesophageal ganglion, may cause inhibition of respiratory

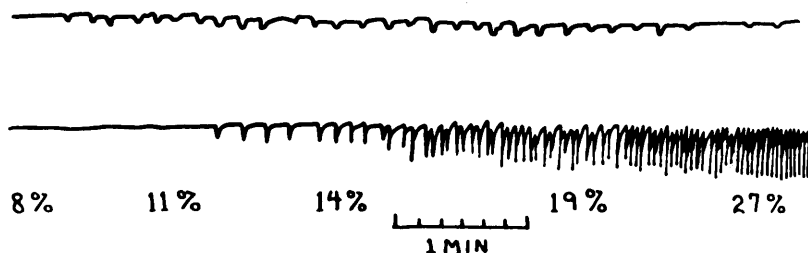


FIGURE 4. (upper line). Spirogram of continuous breathing by the isolated abdomen of *Byrsotria*. (lower line) Increase in respiratory rate of the isolated abdomen brought about by higher percentages of respired carbon dioxide.

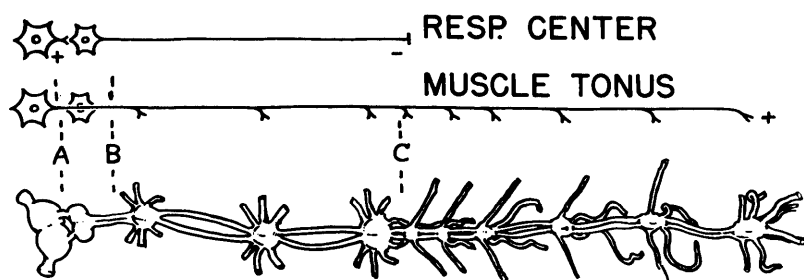


FIGURE 5 (upper diagram). Postulated control of abdominal respiratory center by brain and subesophageal ganglion. Nerve cord section at A removes excitatory impulses from brain, lessening inhibition of the respiratory center by the subesophageal ganglion. Section of cord at B eliminates inhibition of respiratory center. Section at C has same result as section at B.

(middle diagram) Control of muscle tonus of thorax and abdomen by direct brain facilitation. Section of cord at A, B, or C eliminates this control, decreasing body tonus and exaggerating movements.

(lower diagram) Central nervous system of *Byrsotria* showing, from left to right, brain, subesophageal ganglion, three thoracic, and six abdominal ganglia.

impulses from some abdominal center. Removal of the brain could decrease this inhibition by lowering the activity of the subesophageal ganglion (fig. 5, cut at A). This partial release would then result in an intermittent respiratory pattern which is termed periodic breathing.

The repetitive characteristic of these movements is thought to be due to uninhibited proprioceptor feedback mechanisms which serve to re-excite the respiratory center. Similar conditions have been suggested by Bethe (1897) and have been demonstrated by Roeder (1937) in the *Mantis*, which will perform continuous walking movements until halted by fatigue.

Decapitation produces respiratory effects similar to those of decerebration except that periods of apnea virtually disappear; the resulting pattern is that of continuous, slow, high amplitude ventilatory contractions (fig. 3). Section of the

nerve cord between the metathoracic and first abdominal ganglia produces the same respiratory effect (fig. 5, cut at C). These studies indicate, as we have said, that removal of the brain decreases subesophageal inhibition, causing slow periodic breathing with shorter periods of apnea than in the normal roach, but removal of both brain and subesophageal ganglion by decapitation removes all inhibition from the respiratory center (fig. 5, cut at B) causing nearly constant breathing movements.

Exaggerated amplitudes of respiratory contractions seen after removal of cephalic nerve centers may be caused by changes in frequency and duration of respiratory impulses from the respiratory center. Coupled with this may be an augmenting effect on contraction brought about by loss of tonus in the abdominal musculature. Loss of tonus, for example, amplifies walking movements in decerebrated insects and causes circus movements towards the intact side of insects that are unilaterally decerebrated.

The abdomen of the Cuban cockroach is capable of coordinated ventilatory movements after it is separated from the thorax. These movements resemble those of decapitated roaches except that they are of lesser amplitude and the brief periods of apnea are somewhat more frequent. When the isolated abdomen is subjected to increases of CO_2 , an increase in both the respiratory rate and amplitude of respiratory contraction is evident (fig. 4).

It is apparent that the origin of respiratory movement in *Byrostris fumigata* lies in the abdominal ganglia. These ganglia also control the rate and amplitude of breathing in response to increasing partial pressures of CO_2 . Nerve centers of the head, however, exert a regulatory control over breathing movements in the intact cockroach.

SUMMARY

Spirograms recorded from the Cuban burrowing cockroach, *Byrostris fumigata*, demonstrate its normal breathing movements and the spontaneous contractions of the abdomen which are brought about by nerve ganglion extirpation.

Ventilation of intact female roaches consists of slow respiratory movements which occur in short groups separated by long periods of apnea. After brain excision more respiratory movements appear per group, periods of apnea are reduced in duration, and contraction amplitude is increased. Decapitation produces an exaggerated pattern of breathing which is almost continuous. This slow spontaneous ventilatory action is interrupted occasionally by a brief period of apnea. The isolated abdomen continues this latter type of ventilation and is able to modify its rate in response to variations in respired carbon dioxide.

The site of the respiratory center is within the abdominal portion of the nervous system.

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